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Original Research Article

Effects of roadside edge on nest predators and nest survival of Asian tropical forest birds

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ABSTRACT

Creation of roadside forest edges can have indirect effects on forest bird communities, as edges can promote species detrimental to forest-nesting birds such as nest predators. We assessed species-specific rates of nest survival of understory birds, relative abundances of specific nest predators and predator-specific rates of nest predation relative to the distance from roadside forest edge in a dry evergreen forest in northeastern Thailand. During the breeding seasons (February–August) of 2014–2016 we searched for nests along two, 1-km transects which ran perpendicular from the edge of a five-lane highway into the forest interior. To assess nest predator species, video cameras were placed on active nests of understory birds and multiple techniques were used to assess the relative abundances of the documented nest predators. We found 306 active nests of 26 species and recorded 179 predation events from 13 species of nest predators. Distance to edge influenced the daily nest survival rates for four of seven focal bird species, with three species having higher survival rates nearer to the edge. Four of six predators had higher relative abundances in the forest interior. Rats and the Common Green Magpie (*Cissa chinensis*) had higher abundances nearer the edge. Snake detections were too few to assess statistically. Nest predation rates for the top three predators, Northern Pig-tailed Macaque (*Macaca leonina*), Green Cat Snake (*Boiga cyanea*) and Crested Goshawk (*Accipiter trivirgratus*) were significantly greater in the forest interior. The fourth-most important, Common Green Magpie, was the only predator responsible for more nest predation events closer to habitat edge compared to interior. Our study suggests that the impacts of edges on nesting success are highly dependent on the nest predator community and the species-specific responses of predators to edges.

1. Introduction

In the coming decades it is projected that infrastructure development, especially paved roads, will greatly increase, and 90% of these new paved roads will be constructed in developing regions, especially Southeast Asia (Alamgir et al., 2017; Laurance et al., 2015). Roads can have a wide variety of effects on wildlife communities and natural landscapes (Alamgir et al., 2017) but the majority of the impacts are typically deleterious to native species (van der Ree et al., 2015). Roadside edges alter

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the physical environment of forest habitats changing vegetation structure along edges, in conjunction with increased noise and risk of mortality from collisions with vehicles, which may impact populations, distributions, and behaviors of some bird species and their nest predators (Cox et al., 2012; Halfwerk et al., 2011; Jack et al., 2015).

Several nest predators, (e.g. raptors, snakes and small mammals) use edge habitats for foraging, leading to increased predation rates closer to edge areas in at least some regions (Blouin-Demers and Weatherhead, 2001; Cox et al., 2012; Frey and Conover, 2006). However, edge effects on nest predators and nest survival may be species or nesting guild-specific (Flaspohler et al., 2001). Because nest predation is often the primary cause of nest failure (Newmark and Stanley, 2011), thus increases in predation rates may eventually result in reductions of bird populations or local extinctions (Lahti, 2001). However, the effects of forest edge on nest predation seems to vary from site to site within and/or among regions; most data from temperate areas has shown at least some evidence of the negative effects of forest edge on nest predation (Cox et al., 2012; DeGregorio et al., 2014) although others found only weak or no effects (Aldinger et al., 2015; Ruffell et al., 2014). The few studies using natural nests from the tropics tend to show unclear or reverse edge effects, with lower nest predation rates closer to forest edges compared to forest interiors (Spanhove et al., 2014; Visco and Sherry, 2015).

Habitat preferences by nest predators are likely to be species-specific; different species of nest predator are likely to use edge habitats for different purposes and different edge types may attract different nest predators. For example, raptors associated with open habitats may utilize utility poles or power lines along road edges, which they can use to increase visibility for hunting (DeGregorio et al., 2014). Snakes may prefer edge areas where they can also gain thermal benefits from edge habitats (DeGregorio et al., 2014). In addition, small to medium-sized mammalian nest predators (e.g. raccoons, rats) can use edge habitats as travel paths to adjacent habitats (e.g. agriculture areas, human settlements) (Frey and Conover, 2006; Salek et al., 2013). However, other nest predators, particularly forest-dwellers including some squirrels, forest raptors and monkeys, may prefer the forest interior rather than the forest edge (Carlson and Hartman, 2001; Spanhove et al., 2014). Thus, predator responses to edges may not be generally predictable, especially in the tropics where nest predators are mostly unknown.

Researchers often use artificial nests (Batary et al., 2014; Bateman et al., 2017; Malzer and Helm, 2015; Nana et al., 2015) to provide sample sizes needed to make inferences regarding nest success and patterns of nest predation. However, artificial nests have different survival rates and predators than natural nests (Faaborg, 2004; Thompson and Burhans, 2004). Moreover, identification of nest predators using evidence such as teeth marks on artificial eggs or footprints around artificial nests is often unreliable (Faaborg, 2004; Melville et al., 2014). Here, we fill a knowledge gap regarding the influence of tropical forest edge on nest survival, nest predators, and spatial patterns of nest predators using natural nests.

Our objectives were to (1) identify species of nest predators and assess the relative abundance of potential nest predators relative to distance to road edge, (2) assess daily survival rates of understory nests and (3) determine how predator-specific rates of predation respond to roadside forest edge, as well as seasonal factors (rainfall) and nest-site characteristics (nest height). We hypothesized that the composition of the predator community would have a dynamic response to forest edge, perhaps in contrast to a general expectation of lower levels of nest survival near forest edges (Cox et al., 2012). Given our knowledge of the local predator community, we predicted a complex array of spatial patterns with respect to forest edge resulting from a mix of interior (e.g., Northern Pig-tailed Macaque [*Macaca leonina*], Albert et al., 2014) and edge (e.g., rats) specialists. Forest interior species such as Northern pig-tailed Macaques would have lower predation rates at the edge compared to predators which prefer edge or open habitats like snakes and rats. In addition, we evaluated hypotheses regarding the effects of rainfall and nest height on nest survival and nest predation rates, because these variables might influence the foraging behavior and/or foraging success of nest predators. We predicted that (1) predation rates of snakes and Northern Pig-tailed Macaque would rise with increasing rainfall because more rainfall is likely to increase food availability resulting in higher activity levels (Jose-Dominguez et al., 2015a; Marques et al., 2000; Post et al., 1999) and (2) ground/low nests would have lower survival rates because ground/low nests are more accessible and visible to predators (Batary and Baldi, 2004; Ludwig et al., 2012) especially ground/semi-terrestrial predators such as snakes, Northern Pig-tailed Macaque and rats. Artificial nest studies suggested lower success for ground nests (Wilcove, 1985; Ludwig et al., 2012), however artificial nests may not be reliable indicators (Weidinger, 2001). One study using natural nests also suggested lower success for ground nesters (Flaspohler et al., 2001); Martin (1993) observed a similar pattern in grassland habitats, but the opposite pattern in forest habitats.

2. Material and methods

2.1. Study site and study design

This study was conducted in the Sakaerat Environmental Research Station (SERS), classified as a UNESCO Biosphere Reserve in 1977. SERS is part of the Phuluang Non-hunting area covering 160 km^2, located in northeastern Thailand (14°30′N and 101°55′E) at an elevation range of 280–762 m asl. The average annual rainfall is 1200 mm with a dry season from November to April (average rainfall 220 mm) and a wet season from May to October (average rainfall 920 mm), with rainfall peaking in May and September. The average temperature is 27 °C, ranging from 19 to 36 °C. SERS is surrounded by a 5-lane highway to the south, villages and agricultural land to the east and west and the north is connected to a reservoir created by the Lam Phra Phloeng Dam. SERS has two major vegetation types dry-evergreen forest (70%) dominated by tree species *Hopea*

ferrea (Dipterocarpaceae) and *Hydnocarpus ilicifolia* (Flacourtiaceae), and dry-dipterocarp forest (20%) dominated by common dipterocarps such as *Shorea siamensis* (Dipterocarpaceae) and *Shorea obtusa* (Dipterocarpaceae), with the rest of the area comprised of small patches of bamboo, plantations and grassland. Our data collection regarding nest survival and predators of bird nests was conducted within the dry evergreen forest at elevations ranging from 355 to 523 m asl within a kilometer from the forest edge. The edge of this site we defined as "hard" in the sense that the forest ends abruptly and sharply at a five-lane highway (Route 304) (Fig. 1).

We defined the area within 200 m of the highway as forest edge because the vegetation structure in this area was significantly different from the forest interior, with only one or two layers of dense small-diameter trees and saplings and a greater cover of vegetation near ground level (Khamcha et al., 2018). Moreover, the traffic noise was substantial within 100 m of the highway (mean maximum ambient noise = 75 dB) (Khamcha et al., 2018). The rest of the area beyond 200 m from the highway was defined as forest interior.

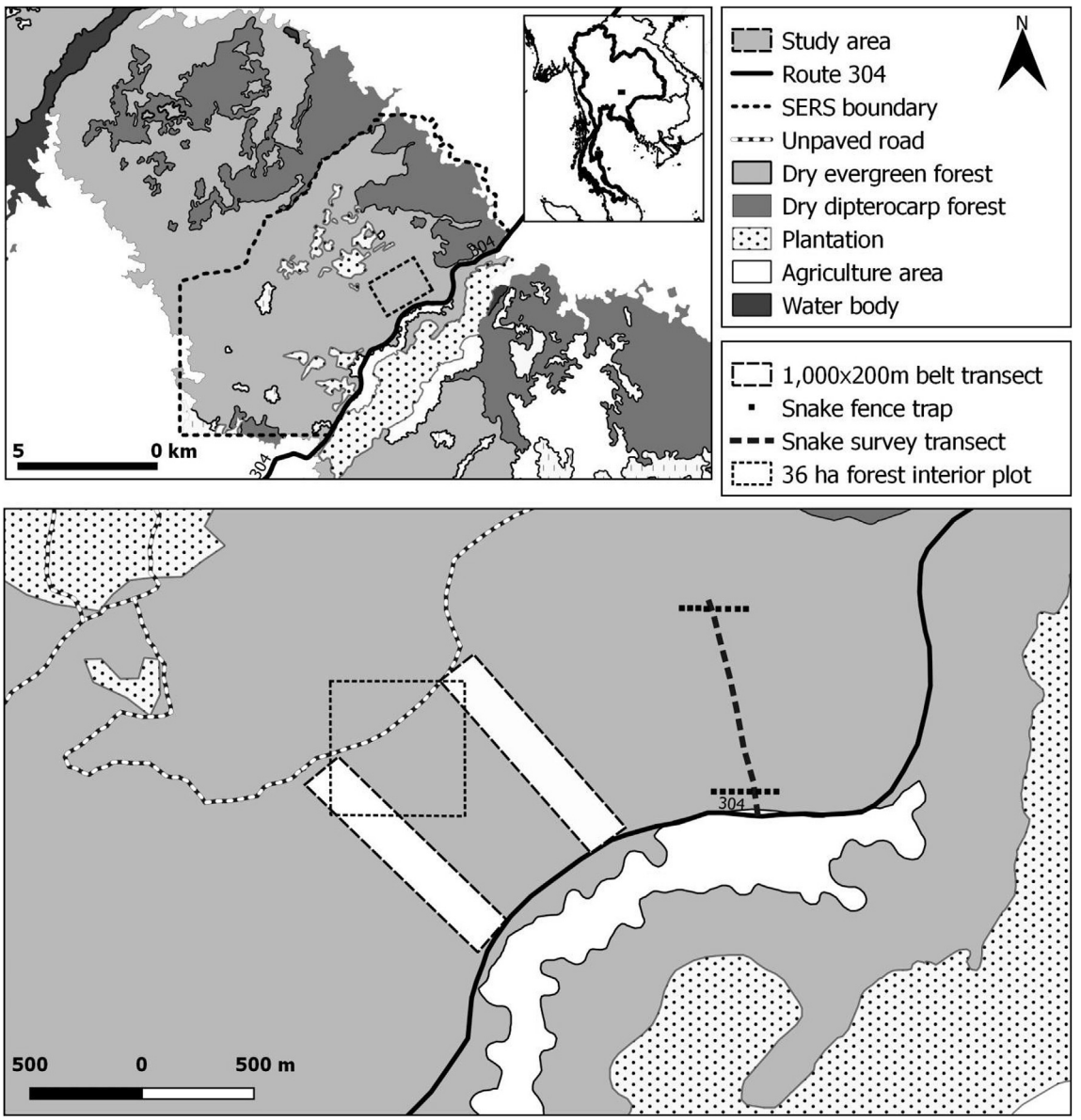

Fig. 1. Predator survey and nest searching locations of the study area located along the edge of the Sakaerat Environmental Research Station, Thailand in 2014–2016. Insets show the area's location in Thailand (upper right), the boundary of study area and landscape context (upper) and details of the study area including the road edge (Route 304), belt transects for predator and nest surveys and transect for night surveys and locations of snake traps (below). Note that the unpaved road inside the study area is a small dirt road only 3 m in width and occasionally used (1–2 vehicles/day).

We used an intensive monitoring scheme consisting of (1) video cameras on active bird nests to identify nest predators and estimate nesting success, (2) stratified sampling with camera traps at the edge and interior areas to assess the relative abundance of mammalian nest predators (e.g., macaques, civets, rodents etc.), (3) point count surveys to assess relative abundances of avian predators (raptors and magpies), (4) live-trapping to identify the species of small-mammalian predators, and (5) drift fences as well as (6) nighttime line transect surveys to assess the relative abundances of snakes.

2.2. Nest finding and nest monitoring

During the breeding season from February to August during 2014–2016 we searched for nests systematically or using behavioral cues following individuals or groups of birds in the study areas within two 1000 × 200 m belt-transects separated from each other by 500 m and located perpendicular to the forest edge (Fig. 1). Once nests were found; species, location, distance from nearest edge, nest type (open cup, dome, plate, and open cavity [shallow cavities in rotten stumps or branches in which an incubating/brooding adult bird is at least partly visible]), nest height and nest stage were recorded. All active nests were monitored every 2–5 days, depending on species and nest stage. Nests of common species that build nests on the ground or in the understorey (0–8 m) which could be reliably video monitored, including Abbott's Babbler (*Malacocincla abbotti*), Black-naped Monarch (*Hypothymis azurea*), Puff-throated Babbler (*Pellorneum ruficeps*), Puff-throated Bulbul (*Alophoixus pallidus*), Scaly-crowned Babbler (*Malacopteron cinereum*), Tickell's Blue-flycatcher (*Cyornis tickelliae*) and White-rumped Shama (*Kittacincla malabaricus*), were monitored 24-h/day using generic waterproof infrared security video cameras with an internal 32 GB micro SD card recorder and mini-microphone. We used a 12-V deep-cycle battery (15AH) as a power source for each camera. Cameras were fastened to trees at least 1.5 m from the nests and camera batteries were placed at least 5 m from nesting areas. We tended to cameras every two days to replace the SD memory card and replaced the batteries every four days. This monitoring system was adapted from Pierce and Pobprasert (2007) and Pierce and Pobprasert (2013). Cameras were setup at active nests only (containing at least one egg) to reduce chances of nest abandonment and were left in place until nest fates were identified. Successful nests were defined from the recorded footage or the appearance of at least one fledgling around the nest-site, while for unsuccessful nests, the cause of failure was also identified from the footage and the presence of eggshells around the nest, destroyed nest remains, missing clutch/nestlings and abandoned clutch/nestlings based on the age of the contents and known fledging periods.

2.3. Nest predator identification and nest predation assessments

Nest predators were identified using recorded footage from the video cameras at active nests. Video cameras allowed us to identify nest predators directly and assess the actual frequency that particular nest predators depredate nests. As we were interested in examining the whole community of nest predators in our study area in the dry evergreen forest, we included data from 112 similarly monitored nests (collected in 2014–2016) from a parallel study being conducted in a 36-ha forest permanent plot in SERS. This 36-ha plot was located between our two belt-transects, 450–1300 m from the forest edge (Fig. 1).

2.4. Nest predator counts

Camera trapping – Potential nest predators of SERS had been at least partly documented prior to our study based on a relatively small sample of video monitored nests from a parallel project in SERS in 2013 and a larger three-year (2006–2008) study by Pierce and Pobprasert (2013) conducted 60 km away in wet evergreen forest. Targeting these known predators, 16 ground-level camera traps, each with a white incandescent flash and a passive infrared trigger (ScoutGuard SG565FV-8M), were placed on the two, 1-km transects used for nest searching noted above (eight camera traps/transect); eight cameras within 200 m from the edge and eight cameras in the interior between 850 and 1000 m from edge, each camera trap in each area was 50 m apart. Camera trapping was conducted during three breeding seasons from March to August in 2014–2016. The camera trap systems were set up to run continuously 24 h per day and to take three consecutive photos per detection, all SD cards from camera traps were retrieved every 15 days. We defined independent events as consecutive photographs of individuals taken more than 30 min apart (O'Brien et al., 2003).

Live trapping – Live trapping was conducted twice, once during the early breeding season (March) and once during the late (August) breeding season of 2015 in order to identify species of rats in the study area. Twenty wire live-traps (18 × 35 × 18 cm) were placed on the two, 1-km transects used for nest searching noted above (one transect at a time). Ten traps were placed in the interior (850–1000 m from the edge) and 10 traps at the edge (within 200 m from edge) each trap in each area was 15 m apart; traps were set for 4–5 consecutive days per transect. We used coconut mixed with peanut butter as bait during the sample periods to increase the probability of capture. All traps were checked once daily in the morning between 0700 and 1000 h. Trapped rats were identified to species and marked with spray paint on the left hind leg before being released. Weight, body length and tail length were also measured, and if available unique marks (e.g., scars) were also recorded.

Nighttime line transect surveys – Night line transect surveys focusing on snake nest predators (i.e., Green Cat Snake (*Boiga cyanea*), Grey Cat Snake (*B. siamensis*) and *Dryocalamus* sp. [Bridle Snakes]) were conducted during May to August 2016 along

a 1 km transect set up perpendicular to the edge, 500 m to the east of the nest searching transects (Fig. 1). The survey was divided into a session of five consecutive days of survey and then stopped for seven days to reduce the disturbance which might affect snake behavior. Each survey was conducted by one observer for 1–2 h between 1900 and 2200 h. All snakes were identified in the field, and then their locations and distances to the nearest edge were recorded.

Drift fence snake traps – 16, 20-m drift fences with two traps on both ends of each fence were set up during May–August 2016; eight fences at the edge (100 m from edge) and eight fences at the interior (900 m from edge) (Fig. 1). Each fence was 20 m apart. All traps were opened for seven days and then closed for seven days to reduce the disturbance around the trap areas. Each trap was checked between 0700 and 1400 h and cleaned after each check. All traps were placed in the shade of trees and were covered by plastic sheets to protect the animals in the traps from direct sunlight. Once snakes were trapped, they were identified and released except the target species (i.e., Green Cat Snake, Grey cat Snake and *Dryocalamus* sp.) which were brought back to the lab for individual marking and measuring by a team of herpetologists working in SERS in collaboration with us, and then released back within 100 m of where they were trapped the next morning. Furthermore, we also set up three baited snake traps during May to August in 2015 at the edge (50 m from edge), at middle distances (500 m from edge) and forest interior (950 m from edge) using fresh quail eggs as bait. However, the baited traps failed to capture any snakes.

Point counts for avian nest predators – In February to August 2014–2015 we conducted bird surveys using point-counts along the same two parallel transects used for nest searching (8 points/transect). The points were arranged to sample a gradient of distances 0 m, 120 m, 240 m, 360 m, 480 m, 600 m, 720 m, and 840 m from the edge. Each point was surveyed for 10 min once every month. The surveys were conducted by one observer between 0600 and 0900 h. All species of birds detected were recorded. The detections were recorded as either seen or heard or both (see Khamcha et al., 2018 for additional description of the bird surveys).

2.5. Data analysis

Influence of key variables on nest survival and nest predation – We used a nest survival model in Program MARK 8.2 (Dinsmore and Dinsmore, 2007) via Program R version 3.4.1 (R Development Core Team, 2017) with package RMark (Laake, 2013) to construct models to estimate daily survival rates (DSR) of nests and to evaluate the effects of the forest edge and other potentially important variables on DSR. Variables for the full set of models included distance from forest edge, nest height and total monthly rainfall. These variables were expected to influence nest predator foraging behavior and activity levels, the variation in predator behavior and activity can be important determinants of nest survival (Cox et al., 2012; DeGregorio et al., 2016; Ludwig et al., 2012; Post et al., 1999). We used total monthly rainfall calculated from two weeks before and two weeks after the predation events occurred or the date of the last nestling fledged for the analysis as we expected seasonal, but not daily or weekly, responses to rainfall by the main nest predators (Northern Pig-tailed Macaque and Green Cat Snake) based on detailed behavioral observations from SERS or nearby (Jose-Dominguez et al., 2015a, N. D'souza, unpublished data). We included year in our preliminary analysis, but excluded it from the final analysis as we found no support for year or day of year affecting DSR or predation rates. We also excluded temperature from the analysis because in our study area especially during the breeding season, average monthly temperature variation was minimal. Distance to edge of each nest was measured using GPS and nest height was measured when the nests were found. Total monthly rainfall was collected from 5 weather stations located within a 2-km radius of the study area. We analyzed daily survival rate and constructed nest survival models for seven focal species individually; species were selected based on whether we had a sufficient number of monitored nests (Table 1). To evaluate the tested variables effects on the predation rates of a given nest predator species, we used generalized linear models (GLMs) with linear and quadratic terms. Our response variables were the proportion of predation events (based on number of cameras) attributed to the main nest predators. We focused on only those species that accounted for >10% of all predation events: Green Cat Snake, Northern Pig-tailed Macaque, Common Green Magpie (*Cissa chinensis*) and Crested Goshawk (*Accipiter trivirgratus*). We evaluated models containing up to three variables that had significant influence on DSR and that were expected to influence behavior and activity patterns of nest predators, specifically, distance from forest edge, nest height and total monthly rainfall.

Table 1
The daily survival rates (DSR) of seven focal species with ≥16 nests and their nesting period lengths, number of active nests and nest types for determining the effects of roadside forest edge on species-species rates of survival at the Sakaerat Environmental Research Station, Thailand in 2014–2016.

Species	DSR (±SE)	Nesting period (days)	*N* nests	Nest type
Abbott's Babbler *Malacocincla abbotti* (ABBA)	0.868 ± 0.031	29	18	Open-cup
Black-naped Monarch *Hypothymis azurea* (BNMO)	0.948 ± 0.012	27	29	Open-cup
Puff-throated Bulbul *Alophoixus pallidus* (PTBU)	0.908 ± 0.013	26	46	Open-cup
Scaly-crowned Babbler *Malacopteron cinereum* (SCBA)	0.916 ± 0.013	27	46	Open-cup
Tickell's Blue-flycatcher *Cyornis tickelliae* (TBFL)	0.901 ± 0.027	25	16	Open-cavity
White-rumped Shama *Kittacincla malabaricus* (WRSH)	0.885 ± 0.020	26	38	Open-cavity
Puff-throated Babbler *Pellorneum ruficeps* (PTBA)	0.923 ± 0.014	27	39	Dome on the ground

After the DSR for all species combined was calculated, the combined nest success was estimated by raising this pooled DSR to the number of days in the average nesting period based on a weighted average of the nesting periods of all the various species in the dataset.

We used Akaike's information criterion (AIC) for ranking models (Akaike, 1973). We used model averaging to estimate values of parameters across models which were within two delta AICc units of the top-ranked model. We considered the strength of evidence for variables influencing DSR of the seven focal species and predation rates of the four top predators using 85% confidence intervals (Arnold, 2010). We then generated prediction lines for the species-specific rate of survival for the focal species and predator-specific rates of nest predation of the main predators relative to distance to edge, nest height and total monthly rainfall.

Relative abundances of nest predators – A relative abundance index (RAI) for all potential mammalian nest predators was calculated by dividing the number of independent photos by the total number of trap-nights for each camera trap location; RAI was standardized to the number of photographs per 100 trap-nights (O'Brien et al., 2003). Because Northern Pig-tailed Macaque regularly occurred in groups, thus to calculate RAI for this species we multiplied the RAI by the maximum number of individuals detected at each camera trap location. We analyzed differences in RAI between edge and interior for all nest predator species combined and each species separately using 95% confidence intervals.

3. Results

3.1. Nest predator identification

From video cameras set up at 287 natural nests of 20 bird species during the breeding seasons of 2014–2016 (Appendix A) we recorded 179 predation events by 13 nest predator species including three species of snakes; Green Cat Snake, Grey Cat Snake, *Dryocalamus* sp. (all predation events by snakes occurred only at night), four species of avian nest predators; Common Green Magpie (*Cissa chinensis*), Shikra (*Accipiter badius*), Crested Goshawk (*Accipiter trivirgratus*), Asian Barred Owlet (*Glaucidium cuculoides*), one species of primate; Northern Pig-tailed Macaque (*Macaca leonina*) and five species of other mammals; Grey-bellied Squirrels (*Callosciurus caniceps*), Variable Squirrel (*Callosciurus finlaysonii*), Common Palm Civet (*Paradoxurus hermaphroditus*), Northern Treeshrew (*Tupaia belangeri*), Rats/Maxomys (Table 2). From 179 predation events, we found that Northern Pig-tailed Macaque was responsible for the most predation events in our study area accounting for 30% of all predation events followed by Green Cat Snake accounting for 24%, Crested Goshawk accounting for 12% and Common Green Magpie accounting for 11% of all predation events. From these 179 recorded predation events, 165 predation events (92%) were recorded at the nests of seven focal species. For most focal species, there was no single dominant nest predator, however we found that Green Cat Snake was the main predator for White-rumped Shama taking more of this species than expected by chance ($\chi^2 = 9.96$, $P = 0.0016$). Northern Pig-tailed Macaque seemed to be the main nest predator for Scaly-crowned Babbler and Black-naped Monarch but the proportions were not significantly different from expected (Appendix B). When we considered the number of predation events of the top predators with regard to nest stage, we found that each predator depredated on nests differently at different nest stages. Common Green Magpie had roughly equal number of predation events on eggs and nestlings (59% vs 41%, $\chi^2 = 0.800$, $P = 0.371$), while Northern Pig-tailed Macaque was more likely to depredate on eggs (75%, $\chi^2 = 13.755$, $P < 0.001$). Green Cat Snake was more likely to depredate on eggs (65%, $\chi^2 = 3.429$, $P = 0.064$) and Crested Goshawk caused nest predations at higher frequency during the nestling stage (76%, $\chi^2 = 5.762$, $P = 0.016$).

Table 2
Nest predators recorded from video cameras from 179 predation events at 287 nests at the Sakaerat Environmental Research Station, Thailand from 2014 to 2016.

Nest predator		2014	2015	2016	Total
Snakes		8	23	29	60
Green Cat Snake	*Boiga cyanea*	8	15	19	42
Grey Cat Snake	*Boiga siamensis*	0	3	0	3
Bridle Snakes	*Dryocalamus* sp.	0	5	10	15
Avian predators		6	25	15	46
Common Green Magpie	*Cissa chinensis*	2	12	6	20
Crested Goshawk	*Accipiter trivirgratus*	2	11	8	21
Shikra	*Accipiter badius*	0	2	1	3
Asian Barred Owlet	*Glaucidium cuculoides*	2	0	0	2
Mammals		15	23	35	73
Northern Pig-tailed macaque	*Macaca leonina*	12	12	29	53
Common Palm Civet	*Paradoxurus hermaphroditus*	0	3	0	3
Grey-bellied Squirrel	*Callosciurus caniceps*	2	4	4	10
Variable Squirrel	*Callosciurus finlaysonii*	1	1	0	2
Northern Treeshrew	*Tupaia belangeri*	0	1	2	3
Rat/Maxomys		0	2	0	2
Total		29	71	79	179

3.2. Nest predator counts

Potential mammalian nest predators – From 16 camera traps we obtained a total of 7148 trap nights and detected six potential nest predator species: Common Palm Civet, Indochinese Ground Squirrel (*Menetes berdmorei*), Northern Treeshrew, Northern Pig-tailed Macaque, Rat/Maxomys and Squirrels (*Callosciurus* sp.) (Table 3). The most common species detected by camera traps were rats with 640 independent detections from a total 1746 independent detections (731 detections at the edge and 1015 detections in the interior). The average RAI (±SE) across all species was significantly larger in the interior (7.79 ± 0.45) than the edge (4.32 ± 0.34) areas (Table 3). When we considered the RAI between edge and interior separately by species the results indicated that the RAI of Common Palm Civet, Indochinese Ground Squirrel, Northern Pig-tailed Macaque and Squirrels were significantly larger in the interior than the edge, while the relative abundance of rats/Maxomys was significantly lower in the interior (Table 3). The RAI of Northern Treeshrew did not show any trend (Table 3).

The live trapping was conducted during the early breeding season (5–20 March 2015) and late breeding season (6–24 August 2015). From a total of 340 trap nights we captured 81 individuals of five species of small mammals which included Red Spiny Maxomys (*Maxomys surifer*) (30 individuals in the interior and 19 individuals at the edge), Long-tailed Giant Rat (*Leopoldamys sabanus*) (eight individuals in the interior and seven individuals at the edge), Northern Treeshrew (four individuals in the interior and five individuals at the edge), Grey-bellied Squirrel (seven individuals in the interior) and Indochinese Ground squirrel (one individual at the edge). Red Spiny Maxomys seemed to be more frequently trapped in the interior than close to the edge but not significantly different from expected ($\chi^2 = 2.469$, $P = 0.116$). The appearances of the other species were similar between interior and edge and not significantly different from expected.

Snake nest predators – From 750 snake trap-nights, 375 trap nights at the edge and 375 trap-nights at the interior we captured 14 individual snakes; nine individuals at the edge and five individuals at the interior (Appendix C). Of these 14, three individuals were those of the target species; one Green Cat Snake and two individuals of *Dryocalamus* sp. Of the target species, two of them (one Green Cat Snake and one *Dryocalamus* sp.) were trapped in the interior and one *Dryocalamus* sp. was trapped at the edge. Eight of the non-target species were trapped at the edge and only three individuals were trapped in the interior, however the number of captures was not significantly different from expected probably due to the small sample ($\chi^2 = 2.273$, $P = 0.132$).

From 37 nights of line transect surveys, we detected 14 individual snakes including nine individuals from the target species (one Green Cat Snake and eight *Dryocalamus* sp.); and five individuals of non-target species. Six individuals (one Green Cat Snake and five *Dryocalamus* sp.) of the target species were detected in the interior (>200 m from edge) and three individuals (three *Dryocalamus* sp.) were detected within 200 m of the forest edge. For non-target species, we detected three individuals at the edge and two individuals at the interior (Appendix C). With this small sample of target species, we found no significant difference in the pattern of detections between edge and forest interior.

Avian nest predators – During a total of 272 point-count surveys we recorded 18 detections of raptors from four species including Asian Barred Owlet (*Glaucidium cuculoides*), Black Baza (*Aviceda leuphotes*), Brown Boobook (*Ninox scutulata*) and Crested Serpent-eagle (*Spilornis cheela*). The number of raptors detections was significantly higher in the interior (>200 m from edge) than expected by chance ($\chi^2 = 4.5$, $P = 0.034$). For Common Green Magpie, we recorded 35 detections and their detections were significantly higher within 200 m from edge than expected ($\chi^2 = 6.4$, $P = 0.011$).

3.3. Daily nest survival

A total of 4195 h was used to search for nests during the breeding seasons (February to August) of 2014–2016 and we located 306 active nests (containing at least one egg) from 26 species. From these active nests, there were 53 successful nests from 14 species. Black-naped Monarch (10 nests), Scaly-crowned Babbler (nine nests) and Puff-throated Babbler (nine nest) were species with the highest number of successful nests. Predation was the leading cause of nest failure for all species. The daily nest survival rate of all birds combined was relatively low 0.914 ± 0.005 (SE) equaling a combined nest success across the three breeding seasons of approximately 8.4%. There were seven species for which we found enough nests to analyze

Table 3
The relative abundance index (RAI) of nest predators between edge and interior areas at the Sakaerat Environmental Research Station, Thailand. The RAI of nest predators was collected using 16 camera traps which were set for 7148 trap nights during the breeding season from March to August in 2014–2016.

Predator species	Edge			Interior		
	RAI	SE	95% confidence interval	RAI	SE	95% confidence interval
Common Palm Civet[a]	3.05	0.29	2.48–3.62	**6.74**	0.42	5.92–7.56
Indochinese Ground Squirrel[a]	0.98	0.16	0.67–1.29	**3.89**	0.32	3.26–4.52
Northern Treeshrew	0.11	0.06	−0.01–0.23	0.11	0.06	−0.01–0.23
Northern Pig-tailed Macaque[a]	8.54	0.47	7.62–9.46	**22.76**	0.70	21.39–24.13
Rat/Maxomys[a]	**10.94**	0.52	9.92–11.96	7.02	0.43	6.18–7.86
Squirrels[a]	2.32	0.25	1.83–2.81	**6.18**	0.04	6.10–6.26
Averaged across all species[a]	4.32	0.34	3.65–4.99	**7.79**	0.45	6.91–8.67

[a] Indicates a significant difference of RAI between edge and interior and numbers in bold indicates the larger RAI within species.

individually, including Puff-throated Bulbul and Scaly-crowned Babbler (46 nests), Puff-throated babbler (39 nests), White-rumped Shama (38 nests), Black-naped Monarch (29 nests), Abbott's Babbler (18 nests) and Tickell's Blue-flycatcher (16 nests), 232 nests in total (Table 1). Of these seven, Black-naped Monarch had the highest daily survival rate (0.948 ± 0.012) followed by the ground-nesting Puff-throated Babbler (0.923 ± 0.014) (Table 1).

3.4. Influence of distance to edge on daily survival rate

We generated six candidate models for each analysis, including species-specific models for focal species and models examining all species combined (Table 4). Forest edge appeared to influence species-specific rates of survival for four of the seven focal species, Abbott's Babbler, Black-naped Monarch, Puff-throated Babbler and Tickell's Blue-flycatcher with distance

Table 4
Candidate models from model selection for daily survival rates of all bird species combined and seven focal species at the Sakaerat Environmental Research Station, Thailand during the 2014–2016 breeding seasons.

	K	AICc	ΔAICc	w_i
Abbott's babbler				
Distance to edge	2	89.18	0.00	0.41
Distance to edge + Nest height	3	90.16	0.99	0.25
Distance to edge + Rainfall	3	91.26	2.08	0.14
Constant survival (NULL)	1	91.77	2.59	0.11
Nest height	2	93.45	4.27	0.05
Rainfall	2	93.82	4.65	0.04
Black-naped Monarch				
Distance to edge	2	129.82	0.00	0.35
Distance to edge + Nest height	3	130.04	0.21	0.31
Distance to edge + Rainfall	3	131.63	1.81	0.14
Constant survival (NULL)	1	132.61	2.78	0.09
Nest height	2	132.67	2.85	0.08
Rainfall	2	134.61	4.79	0.03
Puff-throated Babbler				
Distance to edge + Rainfall	3	199.17	0.00	0.43
Rainfall	2	199.95	0.78	0.29
Constant survival (NULL)	1	201.13	1.96	0.16
Distance to edge	2	201.66	2.50	0.12
Puff-throated Bulbul				
Constant survival (NULL)	1	251.59	0.00	0.31
Rainfall	2	251.77	0.17	0.28
Nest height	2	253.42	1.82	0.12
Distance to edge	2	253.50	1.91	0.12
Distance to edge + Rainfall	3	253.65	2.06	0.11
Distance to edge + Nest height	3	255.05	3.46	0.05
Scaly-crowned Babbler				
Rainfall	2	245.12	0.00	0.42
Constant survival (NULL)	1	247.05	1.93	0.16
Distance to edge + Rainfall	3	247.07	1.96	0.16
Nest height	2	247.22	2.10	0.15
Distance to edge	2	249.07	3.95	0.06
Distance to edge + Nest height	3	249.09	3.98	0.06
Tickell's Blue-flycatcher				
Distance to edge	2	85.16	0.00	0.35
Distance to edge + Rainfall	3	86.70	1.54	0.16
Distance to edge + Nest height	3	86.77	1.62	0.16
Rainfall	2	87.02	1.87	0.14
Constant survival (NULL)	1	87.09	1.93	0.13
Nest height	2	88.82	3.66	0.06
White-rumped Shama				
Constant survival (NULL)	1	166.36	0.00	0.40
Nest height	2	168.05	1.68	0.17
Rainfall	2	168.11	1.75	0.17
Distance to edge	2	168.40	2.03	0.14
Distance to edge + Nest height	3	170.06	3.70	0.06
Distance to edge + Rainfall	3	170.15	3.78	0.06
ALL species				
Constant survival (NULL)	1	1546.03	0.00	0.36
Distance to edge	2	1547.38	1.36	0.18
Nest height	2	1547.72	1.69	0.16
Rainfall	2	1547.88	1.85	0.14
Distance to edge + Rainfall	3	1549.12	3.10	0.08
Distance to edge + Nest height	3	1549.22	3.20	0.07

to the edge indicated as the most supported or included in the most supported models (Table 4) as well as having significant regression coefficients (Table 5). However, for Tickell's Blue-flycatcher and Puff-throated Babbler support for distance to edge appeared to be modest; for the Tickell's Blue-flycatcher the delta AICc was less than two units (1.93) different from the constant survival model and for Puff-throated Babbler the AIC weight (w_i) was low (0.12) (Table 4). Survival of Tickell's Blue-flycatcher nests increased with increasing distance from the edge, while the other three species nest survival was greater nearer the edge (Table 5, Fig. 2). Since different species were responding differently, distance to edge appeared to have no influence on daily survival rate for all species combined (Table 4, Fig. 2).

3.5. Influence of rainfall and nest height on daily survival rate

Only in two species, Puff-throated Babbler and Scaly-crowned Babbler, rainfall was the most supported model and had significant regression coefficients (Table 4, Table 5). Nest success was positively associated with increased rainfall in the Puff-throated Babbler, while increasing rainfall was associated with decreased nest success in the Scaly-crowned Babbler (Table 5). We found no evidence to support effects of nest height on species-specific rates of survival for any of the focal species (Table 4, Table 5).

3.6. Influence of distance to edge on nest predation

To assess the influence of forest edge on predator-specific rates of predation, we focused on only those species responsible for $\geq$10% of all predation events. By this criterion, the top four predators accounted for 136 (~76%) out of the 179 predation events observed. We found strong evidence to support effects of distance to forest edge on predation events by Green Cat Snake, Pig-tailed Macaque and Crested Goshawk; their predation events increased with increasing distance from the forest edge (Table 6, Fig. 3a). We found some evidence to support the effect of forest edge on predation rates by Common Green Magpie and its predation events appeared to be greater closer to the edge (Table 6, Fig. 3a).

3.7. Influence of rainfall and nest height on nest predation

We found some evidence to support a positive influence of rainfall on predation events caused by Green Cat Snake, their predation events increased with increasing rainfall (Table 6, Fig. 3b). We found no evidence to support the influence of rainfall on predation events by the other three main predators (Table 6, Fig. 3b). We also found no correlation between rainfall and predator activity. Number of trapped small mammalian predators were similar between two trapping periods in March (dry period, n = 40) and in August (wet period, n = 41). For snakes, because of the very low number of detections (n = 9) and captures (n = 3), we could not detect a correlation. However, for Northern Pigtailed Macaque the number of captures from

Table 5
Variables influencing daily survival rates of seven focal species and all bird species combined at the Sakaerat Environmental Research Station, Thailand in 2014–2016.

Parameters	Coefficients (β)	SE	85% LCI	85%UCI
Abbott's babbler				
Distance to edge[a]	−0.5252	0.2435	−0.8745	−0.1758
Nest height	−3.3466	3.1318	−7.8391	1.1458
Black-naped Monarch				
Distance to edge[a]	−0.5785	0.2880	−0.9925	−0.1644
Nest height	−0.3063	0.2222	−0.6258	0.0132
Rainfall	0.1016	0.2193	−0.2136	0.4169
Puff-throated Babbler				
Distance to edge[a]	−0.3690	0.2254	−0.6931	−0.0449
Rainfall[a]	0.3034	0.1662	0.0644	0.5424
Puff-throated Bulbul				
Rainfall	0.3359	0.2568	−0.0334	0.7052
Nest height	0.1247	0.2885	−0.2902	0.5396
Distance to edge	−0.0002	0.0005	−0.0008	0.0005
Scaly-crowned Babbler				
Rainfall[a]	−0.3615	0.1799	−0.6202	−0.1028
Distance to edge	−0.0668	0.2517	−0.4288	0.2951
Tickell's Blue-flycatcher				
Distance to edge[a]	0.6048	0.3363	0.1222	1.0873
Rainfall	−0.2536	0.3443	−0.7477	0.2404
Nest height	−0.8007	1.1113	−2.3951	0.7938
White-rumped Shama				
Nest height	0.1589	0.2779	−0.2404	0.5582
Rainfall	0.1263	0.2405	−0.2192	0.4719
Distance to edge	−0.0031	0.2319	−0.3363	0.3301

[a] Indicates significant influence on daily survival rates.

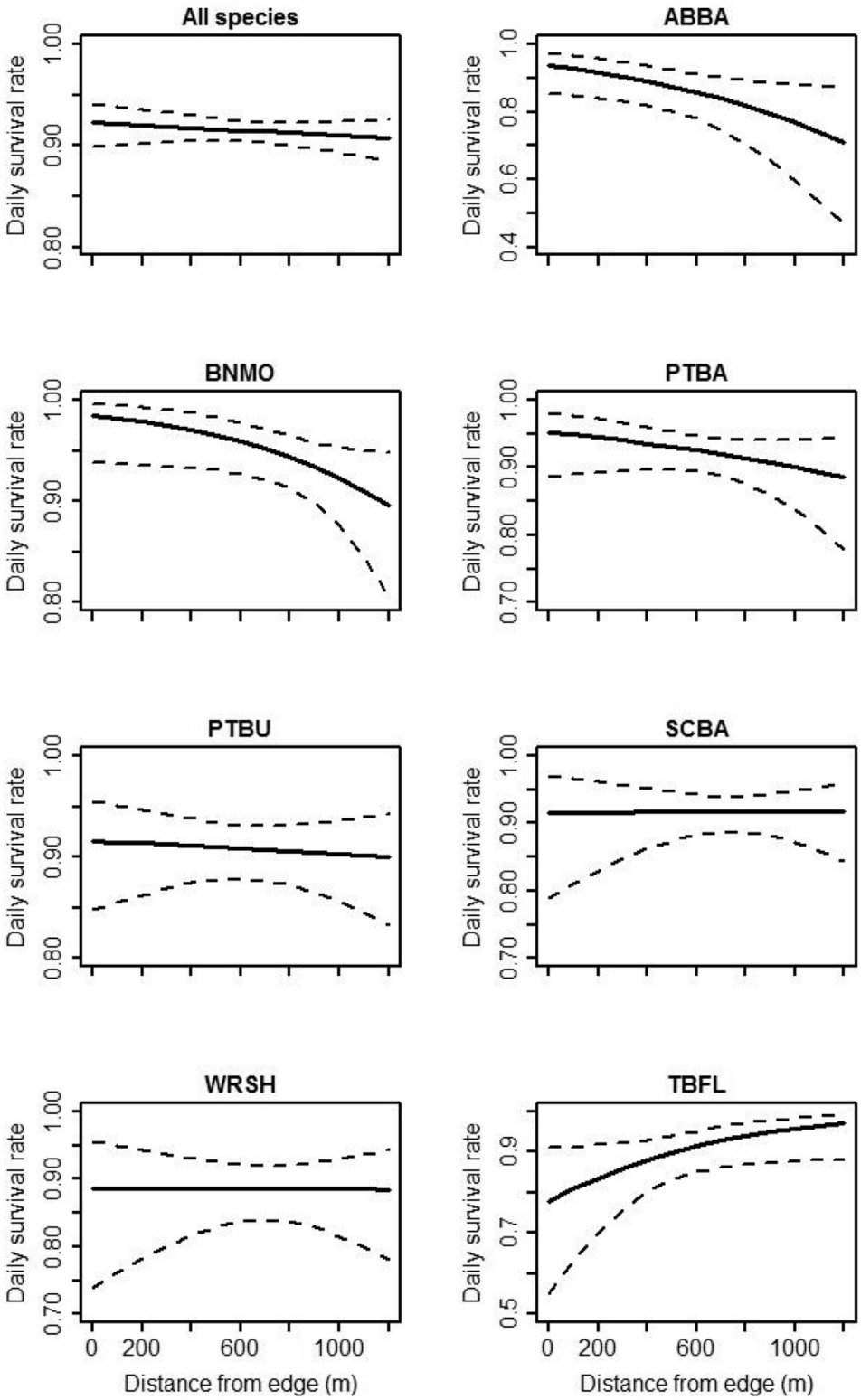

Fig. 2. Modeled daily survival rates (±85% confidence intervals) for seven focal species and all bird species combined as a function of distance to forest edge at the Sakaerat Environmental Research Station, Thailand during the 2014–2016 breeding seasons. ABBA = Abbott's babbler, BNMO = Black-naped Monarch, PTBA = Puff-throated Babbler, PTBU = Puff-throated Bulbul, SCBA = Scaly-crowned Babbler, TBFL = Tickell's Blue-flycatcher, WRSH = White-rumped Shama.

Table 6
Models examining the influence of distance to edge, rainfall and nest height on rates of nest predation by Green Cat Snake, Northern Pig-tailed Macaque, Common Green Magpie and Crested Goshawk; results include estimates of coefficients, standard errors (SE) and 85% confidence intervals (CI) for those three variables at the Sakaerat Environmental Research Station in 2014–2016.

	Model	*df*	AICc	ΔAICc	*wi*	Variable Estimated	Coefficient (β)	SE	Lower 85% CI	Upper 85% CI
Green Cat Snake										
Distance to edge	Edge	2	41.8	0.00	1.00	Edge[a]	0.707	0.199	0.429	1.003
	NULL	1	53.2	11.47	0.00					
Rainfall	NULL	1	54.0	0.00	0.53					
	Rain	2	54.2	0.23	0.47	Rain[a]	0.283	0.170	0.036	0.528
Nest height	NULL	1	42.4	0.00	0.83					
	Height	2	45.5	3.13	0.17	Height	0.059	0.206	−0.246	0.349
Pig-tailed Macaque										
Distance to edge	Edge	2	65.7	0.00	0.86	Edge[a]	0.867	0.196	0.594	1.159
	NULL	1	86.1	20.45	0.00					
Rainfall	NULL	1	58.8	0.00	0.79					
	Rain	2	61.4	2.64	0.21	Rain	0.091	0.167	−0.153	0.329
Nest height	Height + Height^2	3	47.3	0.00	0.94	Height	−0.315	0.315	−0.838	0.094
						Height^2[a]	−0.847	0.273	−1.281	−0.483
	NULL	1	53.4	6.06	0.05					
	Height	2	56.3	8.95	0.01	Height	−0.115	0.201	−0.414	0.169
Common Green magpie`										
Distance to edge	NULL	1	34.5	0.00	0.55					
	Edge	2	34.9	0.43	0.45	Edge[a]	−0.422	0.265	−0.816	−0.047
Rainfall	NULL	1	38.4	0.00	0.74					
	Rain	2	40.4	2.07	0.26	Rain	−0.244	0.270	−0.653	0.129
Nest height	Height + Height^2	3	31.6	0.00	0.59	Height	0.203	0.491	−0.649	0.849
						Height^2[a]	−1.110	0.485	−1.940	−0.500
	NULL	1	32.8	1.20	0.33					
	Height	2	35.6	3.98	0.08	Height	0.196	0.288	−0.244	0.593
Crested Goshawk										
Distance to edge	Edge	2	39.4	0.00	0.73	Edge[a]	0.548	0.259	0.190	0.940
	NULL	1	41.3	1.96	0.27					
Rainfall	NULL	1	34.7	0.00	0.69	Rain	−0.302	0.269	−0.711	0.070
	Rain	2	36.3	1.59	0.31					
Nest height	NULL	1	33.6	0.00	0.83					
	Height	2	36.8	3.12	0.17	Height	0.084	0.267	−0.323	0.453

Edge represents distance to forest edge, Rain is total monthly rainfall and Height represents nest height.
[a] Indicates significant influence on predation events.

camera traps appeared to be related with the rainfall, the number of captures was greater during the wet period (63%) than the dry period (37%) but we found no effect of rainfall on the predation events by Northern Pigtailed Macaque.

We found strong evidence to support the influence of nest height on predation events by Northern Pig-tailed Macaque and Common Green Magpie. Nests at approximately 1–2.5 m height were more frequently depredated by these predators than nests <1 m in height (including ground nests) or nests at heights >2.5 m (Table 6, Fig. 3c). There was no evidence to suggest there was an effect of nest height on predation events by either Green Cat Snake or Crested Goshawk (Table 6, Fig. 3c).

4. Discussion

We found support for our hypothesis that forest edge influenced species-specific rates of nest survival and predator-specific rates of nest predation. Our supported models for species-specific rates of survival indicated positive edge effects on DSR for three focal species and negative effects on DSR of one focal species. Our results also revealed a significant negative influence of edge on nest predation by three of the top four nest predators, the fourth predator (Common Green Magpie) showed a significant positive response to forest edge. Overall, our results indicated that responses to roadside forest edge and other tested variables at SERS appeared to be species-specific.

4.1. Nest predators and nest predation dynamics

We documented a diverse group (13 species) of nest predators, which was similar to the predator community reported in a previous study in a nearby old-growth evergreen forest at Khao Yai National Park (KYNP) (12 species) (Pierce and Pobprasert, 2013). The study by Pierce and Pobprasert was the only previous study of nest predators of natural nests in tropical Asia as far as we are aware. At KYNP, Pierce and Pobprasert (2013) found that Northern Pig-tailed Macaque was the most frequent nest predator accounting for 44% of all predation events followed by Green Cat Snake (22%). In contrast, our study was less dominated by Northern Pig-tailed Macaque, which accounted for only 30% of all predation events followed by Green Cat Snake (24%). We recorded at least three different species of highly arboreal (Chan-ard et al., 2015; Das, 2010) snakes as nest predators (Green Cat Snake, Grey Cat Snake and *Dryocalamus* sp.), and two of them (Grey Cat Snake and *Dryocalamus* sp.) had

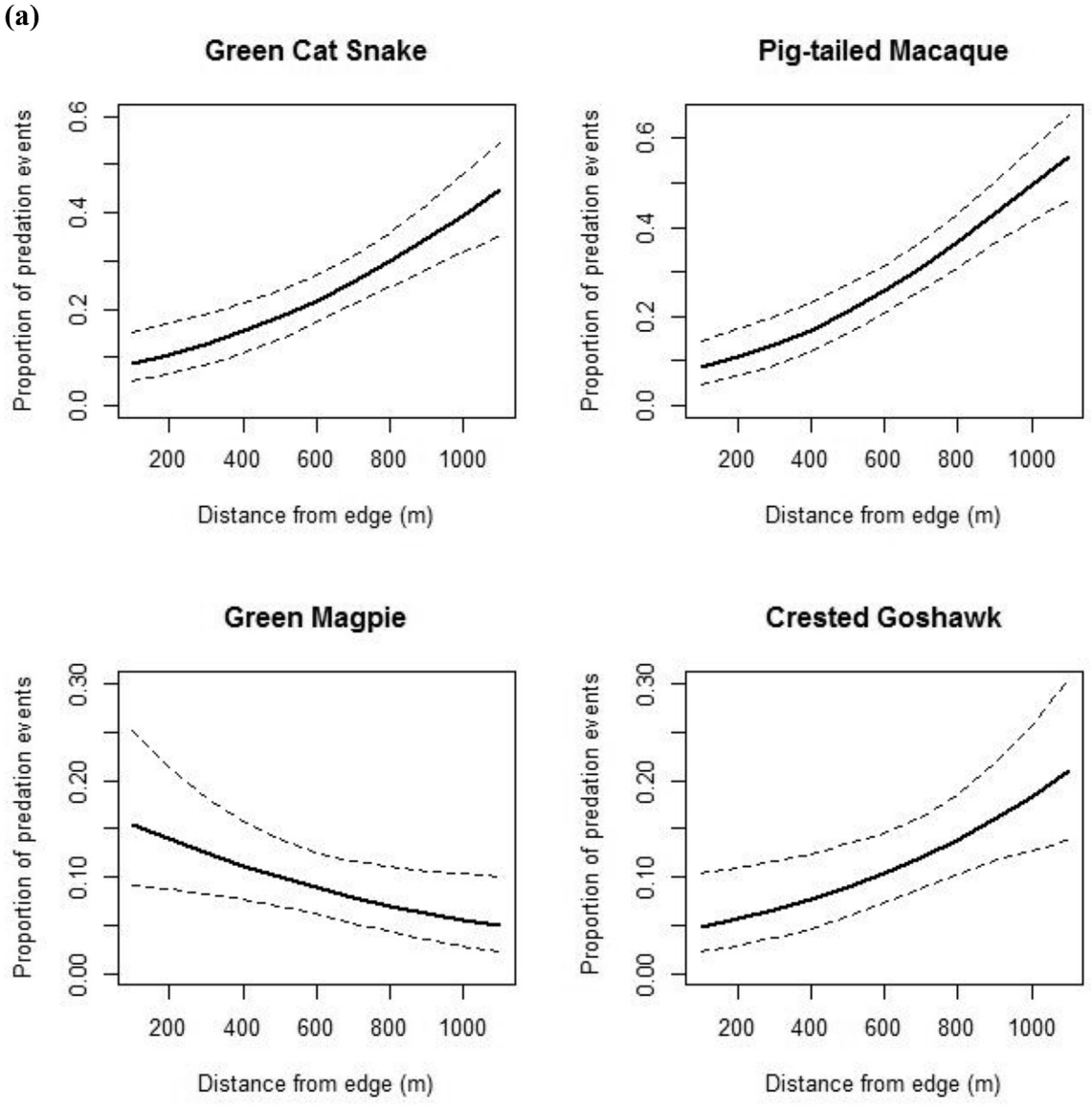

Fig. 3. The predation events caused by four main nest predators; Green Cat Snake, Northern Pig-tailed Macaque, Common Green Magpie, Crested Goshawk as a function of distance from the forest edge (a), total monthly rainfall (b) and nest height (c) at the Sakaerat Environmental Research Station during the breeding seasons of 2014–2016.

not been recorded as nest predators during the KYNP study. These three snake species accounted for 34% of all predation events. The lower proportion of predation events from Northern Pig-tailed Macaque in SERS could be due to a lower density of macaques relative to KYPN or differences in ranging patterns with only one macaque troupe in the SERS study area (E. Gazagne, unpublished data) probably because SERS is relatively small (160 km^2). At the 30-ha study plot in KYNP (>2000 km^2) there may have been at least three groups of macaques ranging in the area (Jose-Dominguez et al., 2015b). Although, the predation rate by Northern Pig-tailed Macaque was lower in SERS, the overall nest success from nests with and without cameras was still low (8.4%) compared to the study from KYNP (16%). Moreover, the nesting success of the focal species with sufficient sample sizes were all lower in SERS compared to KYPN; Abbott's Babbler (1.7% *vs*. 23.6%), Black-naped Monarch (23.8 *vs*. 27.9), Puff-throated Bulbul (8.1 *vs*. 11.0), White-rumped Shama (4.2 *vs*. 29.6), Tickell's Blue-flycatcher (7.3% at SERS) *vs*. Hill Blue Flycatcher (30.9% at KYNP), it seems likely that the reduced predations by Northern Pig-tailed Macaque in SERS was compensated by snakes (Ellis-Felege et al., 2012). The reason for such low nest success and high predation rates is unclear, however the increased proportion of predation events attributed to snakes may be a significant factor. We noted that for birds where snakes were the main predator in SERS (White-rumped Shama, Tickell's Blue-flycatcher vs. Hill Blue Flycatcher), nest success of these species was notably lower at SERS compared to KYNP, whereas the two species depredated less by snakes

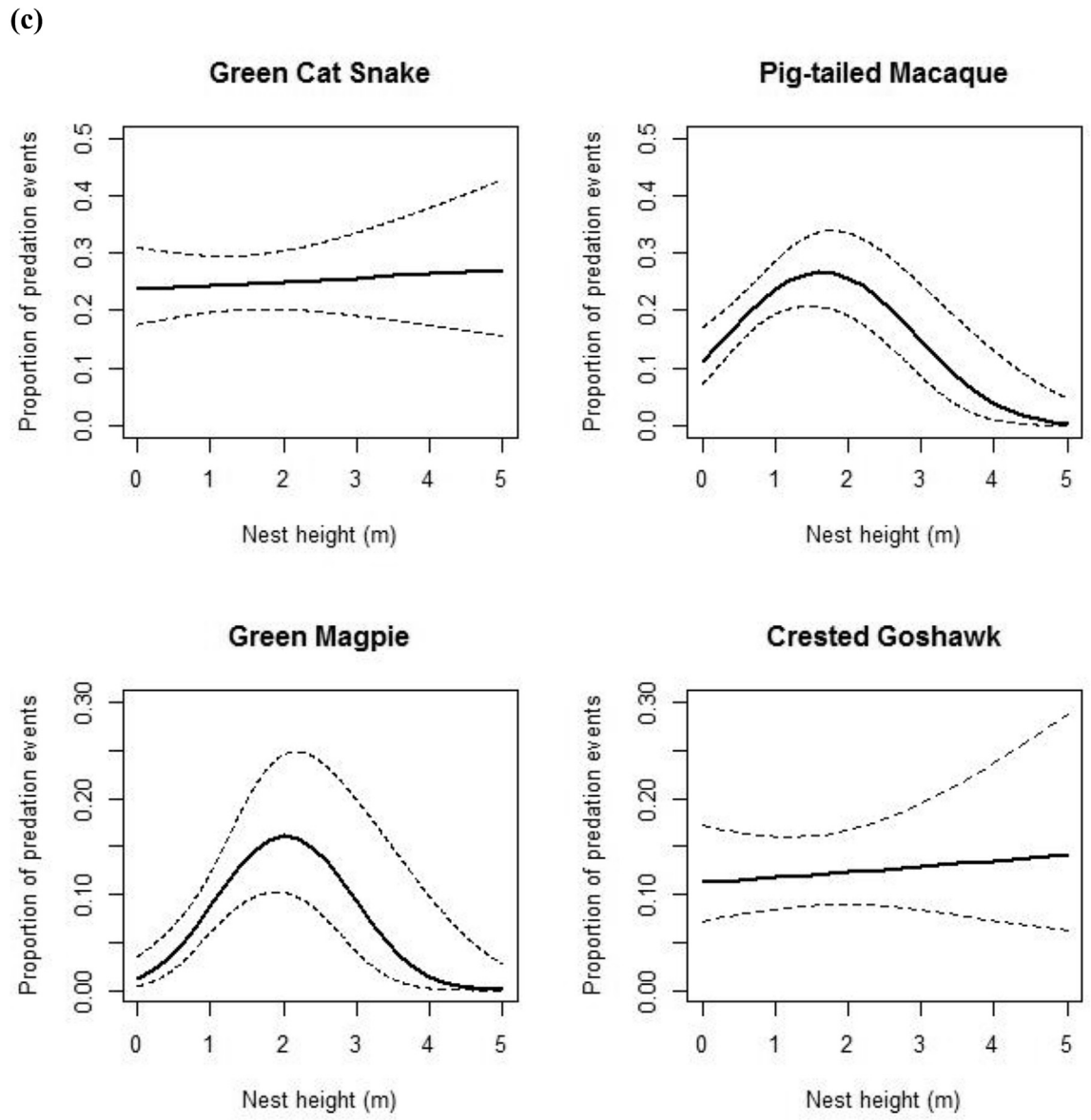

Fig. 3. (*continued*).

Black-naped Monarch and Puff-throated Bulbul had relatively similar DSR between the two sites. The increased predation rates by snakes at SERS may be the result of a relatively lower diversity and abundance of their predators (e.g. raptors, civets, mongooses), although we currently do not have quantitative data to demonstrate this. We also have very limited long-term monitoring data from SERS to assess long-term population trends, although our small marked sample of Scaly-crowned Babblers showed no decline during the past five breeding seasons (2014–2018). While, the overall nest success was low (8.4%) at SERS compared to the other tropical studies (Brawn et al., 2011; Robinson et al., 2000), our focal species can re-nest up to 4–5 times per season which may be sufficient for sustaining at least some populations (Amat et al., 1999).

4.2. Influence of roadside forest edge on daily survival rates

We found support for our hypothesis that forest edge influenced species-specific rates of survival and each predator affected each bird species differently. For four of seven focal species, distance to edge was an important predictor of nest survival and three out of those four positively responded to roadside forest edges (higher survival rates closer to the edge). These results could be explained as a consequence of the relatively lower predation pressure near the edge habitats, similar to results from a few other studies (Angkaew et al. in review, Spanhove et al., 2009; Visco and Sherry, 2015). The increased daily

(b)

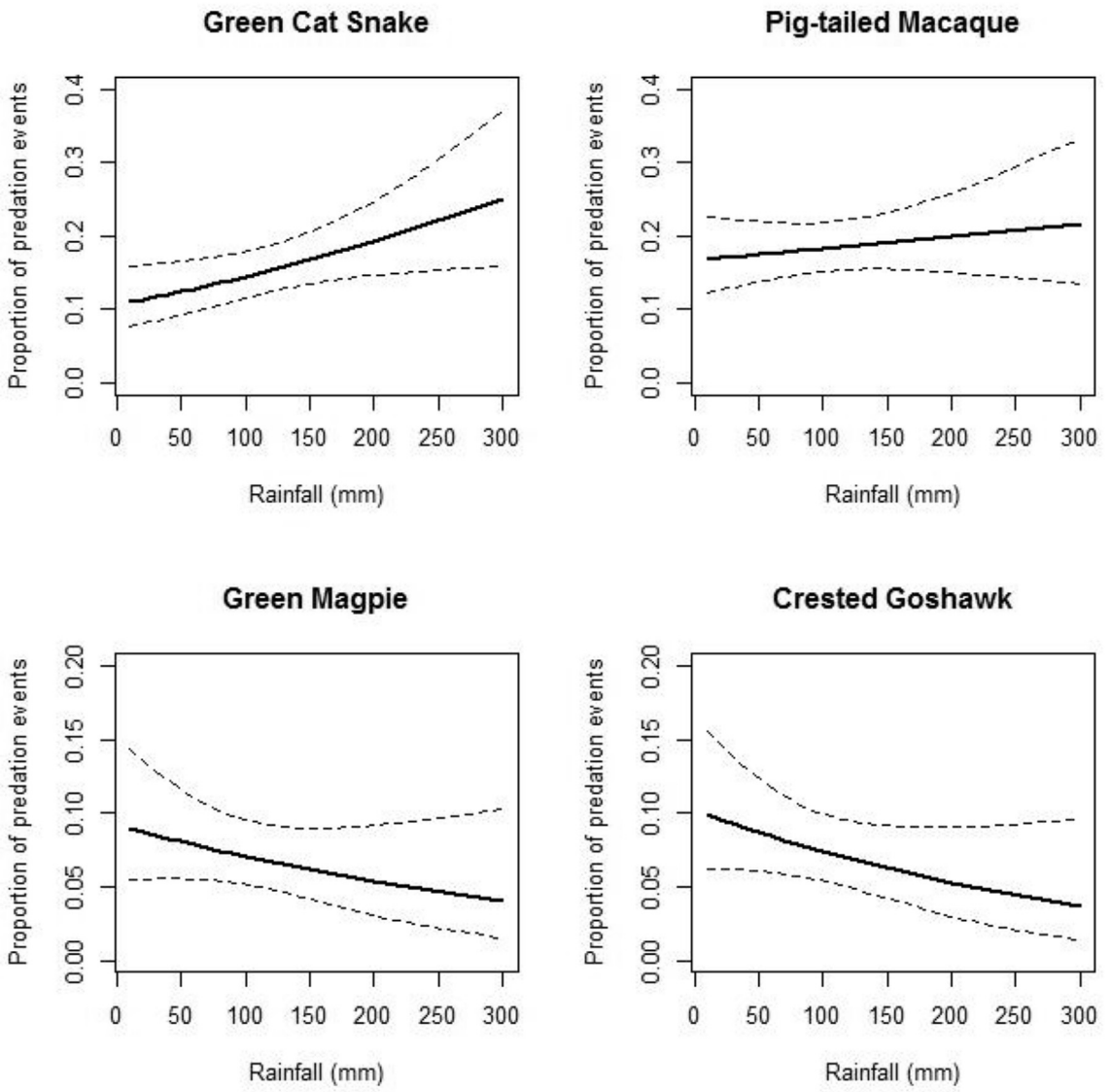

Fig. 3. (*continued*).

survival rates close to edge for most species appeared to be related to the lower levels of foraging activity and relative abundances of their main predators at the edge (Green Cat Snake, Northern Pig-tailed Macaque and Crested Goshawk). In contrast to the other birds, daily survival rate of Tickell's Blue-flycatcher was greater in the forest interior, but the edge associated predator, Common Green Magpie, was probably not their main predator (1 predation event), although the number of predation events video-recorded at Tickell's Blue-flycatcher nests was small (8 events).

We found no response to the forest edge regarding daily survival rates of three focal bird species (Puff-throated Bulbul, Scaly-crowned Babbler and White-rumped Shama) which may incur similar predation rates from both forest interior and edge predators, except for White-rumped Shama which seemed to be depredated by mostly Green Cat Snake at both the interior and the edge.

4.3. Influence of roadside forest edge on nest predators and nest predation dynamics

The responses to forest edge by nest predators were species-specific as we predicted. We documented greater nest predation events by Green Cat Snake in the forest interior, which may be due to preferences for habitat where the vegetation structure was more complex and generally more connected. The forest interior in our study area had a greater density of large

trees and more vegetation layers which may have provided more suitable foraging habitat compared to forest edge (Angkaew et al. in review, Khamcha et al., 2018). Vegetation structure at the edge was generally simpler, with a dense cover of saplings (0.5–3 m in height) and a greater cover of vegetation near ground level (Khamcha et al., 2018). These structural changes at the roadside edge may have negative effects on the foraging habitats of our main predators, causing them to avoid these edge areas (Spanhove et al., 2014). Green Cat Snake is primarily arboreal and shelters in tree cavities; preliminary data suggest that the height of their movements and shelter sites was generally off the ground, but <6 m (N. D'souza, unpublished data). It is possible that lower tree density was associated with lower connectivity at the forest edge impeding their movements (Khamcha et al., 2018). In addition, the greater density of trees in the forest interior could provide relatively more cavities (Lindell et al., 2004; Mahmoudi et al., 2016) for both Green Cat Snake and their cavity nesting prey (especially White-rumped Shama). However, detections and captures of the Green Cat Snake and the other snake nest predators from the drift fences (three individuals) and surveys (nine detections) were insufficient to adequately estimate abundance or relative distributions.

Northern Pig-tailed Macaque also avoided the edge and their predation events were significantly greater in the forest interior. Our surveys also indicated significantly higher RAI of Northern Pig-tailed Macaque in the forest interior. Asian macaques are known to be particularly shy and avoid urban or otherwise human disturbed areas (Albert et al., 2014). The edge in our study was a busy five-lane highway (approximately 950 cars/h) with substantial traffic noise (mean maximum ambient noise = 75 dB) within 100 m from the edge (Khamcha et al., 2018), which may be the main cause of edge avoidance in the Northern Pig-tailed Macaque.

Eighty percent of all predation events by raptors in our study were attributed to Crested Goshawk, a forest-dwelling species (Robson, 2013). Although several studies have reported that nest predation by raptors was positively associated with forest edge or road edge (Cox et al., 2012; DeGregorio et al., 2014), we detected lower rates of nest predation by Crested Goshawk closer to the roadside forest edge. Overall, our point count data indicated more detections of raptors in the forest interior (>80%), suggesting again that edge responses by raptorial predators are probably species-specific.

Common Green Magpie was the only nest predator that had more predation events and a relatively large proportion of detections close (≤200 m) to the edge. Common Green Magpie is a member of the crow family, and a forest generalist found in a variety of habitats within SERS (Salema et al., 2018). This finding was similar to DeGregorio et al. (2014) who observed that nest predations by corvids were greater at edges, and they also considered edges to be the preferred sites for corvids foraging generally. Although, Common Green Magpie is similar to other species in the crow family in its generalist foraging habits (Salema et al., 2018), we had no evidence of Common Green Magpie eats carrion or roadkill.

We found larger relative abundances of several other potential mammalian nest predators including Common Palm Civet, Indochinese Ground Squirrel and other squirrels in the interior as well. As we mentioned above, our busy five-lane highway edge (high traffic volume and noise) and the associated altered habitat (Khamcha et al., 2018) may also account for their edge avoidance. Rats were the only species that had higher levels of abundance at the edge. The larger relative abundance of rats at the edge habitat has also been observed in several other studies (Cox et al., 2012; Ruffell et al., 2014). However, our study also confirmed that potential predators with elevated relative abundances in an area may not necessarily be important in the overall mortality of nests as they may actually prefer other available prey (DeGregorio et al., 2014; Liebezeit and Zack, 2008). Edge-associated mammals (Northern Treeshrew, squirrels and Rat/Maxomys) combined accounted for only 17 (~10%) of the 179 observed predation events in our study (Table 2).

Although, our results should be applicable for assessing the effects of roadside forest edge (vegetation structure and/or possibly traffic noise) on nest predator distributions and behaviors, we caution that predators may respond differently to different edge types, such as narrower roads or roads with lower traffic volumes or edges without roads. One of the few studies that have examined road edges with different traffic volumes found highly variable predation rates among years and among sites with different traffic rates using artificial nests (Pescador and Peris, 2007). Another study using natural nests also found that certain species of nest predators will respond differently depending on the edge type, such as unpaved roads versus power lines (DeGregorio et al., 2014). This further suggests that nest predation rates are highly dependent on specific predators interacting with specific landscapes and that different kinds of edges are likely to generate different levels of responses.

4.4. Influence of rainfall and nest height on nest predators and nest predation dynamics

The Green Cat Snake was the only predator that appeared to respond to seasonal changes in rainfall. The association between increased rainfall and increased predation events by Green Cat Snake is possibly related to the increase of their activity during higher rainfall periods. More rainfall means more food availability such as amphibians (Heinermann et al., 2015) and a greater number of active bird nests, may result in higher activity levels of snakes in general. Preliminary data also suggests that Green Cat Snakes forage more widely outside of the cooler, drier season of the year (N. D'souza, unpublished data). However, the relationship between rainfall and snake activity levels remains equivocal with some studies suggesting that snake activity levels are not related to rainfall (Daltry et al., 1998; Brown and Shine, 2002) while others indicating a positive relationship (Post et al., 1999; Marques et al., 2000). This variation may also indicate that this relationship is region and/or species-specific.

Common Green Magpie and Northern Pig-tailed Macaque appear to more frequently depredate nests 1–2.5 m in height compared to ground/lower or higher nests. This is similar to other studies which found that shrub nests suffered higher predation rates relative to nests outside this stratum (Martin, 1993; Soderstrom et al., 1998). Common Green Magpie had

significantly greater predation rates on nests at 1.5–2.5 m height, which also was the height of the dominant vegetation at the edge where Common Green Magpie had more predation events. The vegetation structure at the edge also had a greater density of saplings and shrubs of 0.5–3 m in height, limiting the heights where nests could be placed. This finding was similar to Soderstrom et al. (1998) who found that corvids accounted for almost all predation events on shrub nests (1.5 m above ground) and this was also their average foraging height. For Northern Pig-tailed Macaque, our findings were consistent with Kaisin et al. (2018) who found that artificial nests at heights >0.5–1 m were more likely to be depredated by Northern Pig-tailed Macaque at SERS compared to nests at heights >1–2 m. Northern Pig-tailed Macaque typically travel on the ground actively searching for food, including nests and can also detect activity of adult birds at nests, although most of the depredated nests were roughly at or below the height of a macaque (<1 m) (Kaisin et al., 2018).

5. Conclusions

Our results indicate the effects of roadside forest edge on nest survival as a consequence of the influence of vegetation structure and perhaps road noise on nest predator distribution and behavior. Our study also raised several interesting issues for managers and researchers. First, we have documented species-specific responses to roadside forest edge, but understanding which mechanisms (e.g., noise, sunlight, temperature etc.) associated with edges are most influential to a nest predator community is also needed to improve conservation management and to mitigate potential impacts from these edges. Second, the interactions among nest predators in the context of creation of new edges that may modify the composition of the predator community is likely to be complex. Snakes may be compensating for lower levels of macaque predation, and compensatory predation must be documented for proper management planning (Ellis-Felege et al., 2012). Finally, the effects of predators in the context of forest edges appears to vary from region to region and also from site to site in the same region as predator communities vary in composition. Responses to forest edge especially roadside forest edge in tropical Southeast Asia may be different from the temperate zone or even other tropical regions. Southeast Asia is considered as the epicenter of infrastructure expansion (Laurance et al., 2015) hence, managing habitat to minimize the impacts, managers will likely need to know who the dominant nest predators are and how these predators are likely to respond to edges regionally.

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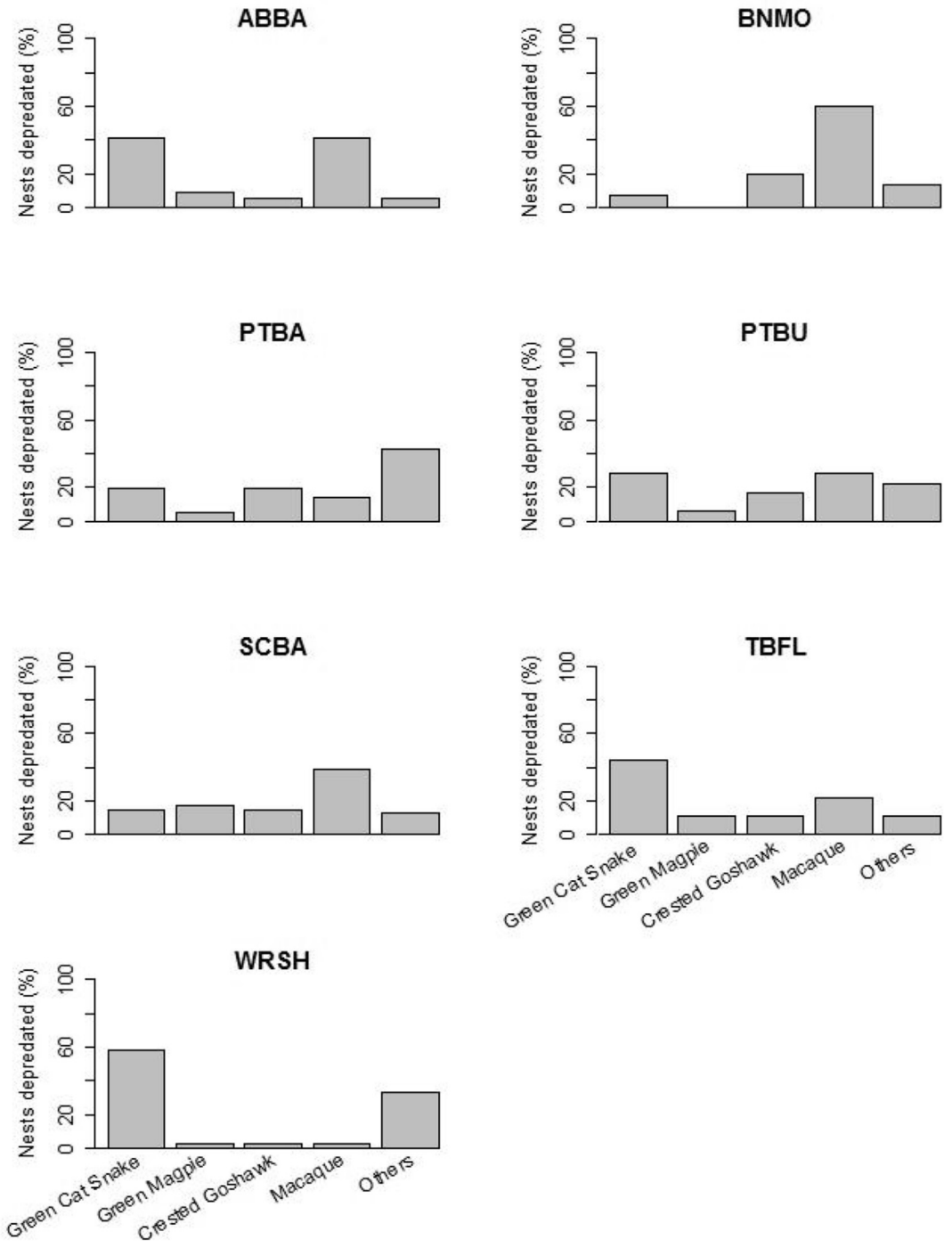
Appendix A. Nests of 20 species of birds monitored using video cameras at the Sakaerat Environmental Research Station, Thailand during the 2014–2016 breeding seasons.

Species	*N* monitored nests	Nest type	Ave. nest height (m)
Abbott's Babbler *Malacocincla abbotti*	22	Cup	0.8
Black-headed BulBul *Pycnonotus atriceps*	2	Cup	1.2
Black-naped Monarch *Hypothymis azurea*	18	Cup	2.4
Common Green Magpie *Cissa chinensis*	4	Shallow cup	6.3
Crimson Sunbird *Aethopyga siparaja*	1	Purse-shaped	2.3
Great Eared Nightjar *Eurostopodus macrotis*	2	Bare ground	0
Grey-capped Emerald Dove *Chalcophaps indica*	2	Platform	1.8
Hainan Blue-flycatcher *Cyornis hainanus*	1	Cup	1.2
Lesser Necklaced Laughingthrush *Garrulax monileger*	2	Shallow cup	2.5
Orange-breasted Trogon *Harpactes oreskios*	4	Open cavity	2.9
Pin-striped Tit-babbler *Mixornis gularis*	3	Loose ball-shaped	2.3
Puff-throated Babbler *Pellorneum ruficeps*	41	Dome, ground	0
Puff-throated Bulbul *Alophoixus pallidus*	25	Cup	2
Red Junglefowl *Gallus gallus*	1	Shallow hollow	0
Scaly-crowned Babbler *Malacopteron cinereum*	69	Cup	1
Siamese Fireback *Lophura diardi*	1	Shallow hollow	0
Stripe-throated Bulbul *Pycnonotus finlaysoni*	18	Cup	1.8
Tickell's Blue-flycatcher *Cyornis tickelliae*	24	Open cavity	1
White-crested Laughingthrush *Garrulax leucolophus*	2	Shallow cup	4.3
White-rumped Shama *Kittacincla malabaricus*	45	Open cavity	2.5

Appendix B. Percentage of depredated nests for seven focal species caused by four main nest predators at the Sakaerat Environmental Research Station, Thailand during the 2014–2016 breeding seasons. ABBA = Abbott's babbler, BNMO = Black-naped Monarch, PTBA = Puff-throated Babbler, PTBU = Puff-throated Bulbul, SCBA = Scaly-crowned Babbler, TBFL = Tickell's Blue-flycatcher, WRSH = White-rumped Shama.



Appendix C. The number of captured snakes from 750 snake trap-nights using 16, 20 m drift fences with 2 traps on both ends and numbers of detected snakes from 37 night line transect surveys on a 1-km transect at the Sakaerat Environmental Research Station in 2016.

Species	Drift fence trap			Night surveys		
	edge	interior	total	edge	interior	total
Target species						
Boiga cyanea	0	1	1	0	1	1
Dryocalamus sp.	1	1	2	3	5	8
Total	1	2	3	3	6	9
Non-target species						
Ahaetulla prasina	0	0	0	1	0	1
Bungarus candidus	1	0	1	0	0	0
Coelognathus radiatus	1	0	1	0	0	0
Dendrelaphis sp.	3	0	3	0	0	0
Gongylosoma scriptum	0	1	1	0	0	0
Lycodon subcinctus	1	0	1	0	0	0
Oligodon sp.	1	2	3	0	0	0
Psammodynastes pulverulentus	1	0	1	0	0	0
Trimereserus macrops	0	0	0	2	2	4
Total	8	3	11	3	2	5
Grand total	9	5	14	6	8	14

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